Ontogenetic and Functional Aspects of the Regulation of Reactions to Natural Auditory Stimuli by Great Tit Nestlings (Parus major)

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The dissertation is based on the following four papers, referred to in the text by the respective Roman numerals:

I Rydén, O. (1972). Habituation of the cease-begging response of Great Tit nestlings (Parus major) to different acoustic stimuli. Psychol. Res. Bull., Lund Univ., XII:7.

II Rydén, O. (1973). Conditioning and extinction of begging to auditory stimuli of differing significance. An experiment with Great Tit nestlings (Parus major). Psychol. Res. Bull., Lund Univ., XIII:9.

III Rydén, O. (1974). Reactions to natural auditory stimuli by wild-captured and partly laboratory-raised Great Tit nestlings (Parus major). Psychol. Res. Bull., Lund Univ., XIV:1.

IV Rydén, O. (1974). Responses to an alarming auditory stimulus as affected by massive earlier exposure. A combined field- and laboratory experiment with Great Tit nestlings (Parus major). Psychol. Res. Bull., Lund Univ., XIV:3.

Introduction

All organisms exhibit a differential responsiveness to stimuli in their environments. Some stimuli evoke vigorous, other weak or no reactions. Avoidance responses, e.g., are differentially activated by stimuli signifying possible danger. For example, a small passerine bird reacts to any sudden, intense or moving stimulus by a transient startle reaction but responds by taking cover and adopting a frozen posture at the sight of a flying predator. These differences in responses, selectively associated with different stimuli, can be assessed by various methods and in various contexts. The method used and the context in which it is applied corresponds with the way in which the obtained observations are interpreted. Generally speaking, two main approaches can be distinguished.

(1) A naturalistic, basically non-manipulatory approach that largely relies on systematic observation of spontaneous behavior in natural contexts. Originating from descriptive accounts of the general behavior of organisms as related to the specific demands of their environments, this approach primarily leads to an evolutionistic consideration of the adaptive value of an observed behavior. Furthermore, this approach is structure-oriented, mostly studying species-specific responses that appear unmodifiable and independent of prior individual experience. It may be added that, although responses are often characterized by their presumed selection-values, these are rarely actually investigated.

In line with this approach, an observed difference in response-strenght as elicited by two stimuli would primarily be interpreted in terms of adaptive consequences. If these are evident in naive animals, e.g. if a predator evokes a more vigorous or more persistant response than a strong but harmless stimulus, a heavy impact of genetic energineering on the development of the observed reactions would be presumed.

(2) A process-oriented, atomistic and experimental, i.e. manipulatory approach, that often disconnects the observed response from its natural context; hence it does not view the response as subordinated to the general behavior of the organism but as illustrating some principle or law within psychological theory. Following this approach, an observed difference in response-strength would be interpreted in terms of stimulus quantity, earlier reinforcement, and stimulus generalization or discrimination. Experiential influences and response-modifiability are stressed.

Adherents of these two approaches, here only briefly described, generally are associated with two originally separate traditions in the study of animal behavior, one confined to the experimental study of psychological processes, the other having its foundation in biology. Although a mutual influence and exchange of ideas have affected the later development of these two approaches, it is still possible to define front-lines, e.g. on the nature-nurture issue and with respect to methodology (Lorenz, 1965). Essentially, continental European ethology is partly still well characterized in terms of the first approach,outlined above, while the development of the American counterpart has been and still is influenced by the behavioristic tradition in U.S. as is clear from the description of the second approach (cf. Schneirla, 1966). British ethology seems to have an intermediate position (Tinbergen, 1969). A quite isolated stand is still held by the learning theorists where the study of animal behavior is primarily a means in their efforts to identify general laws of learning, valid for man as well as for the animal species studied. Although, within this tradition, two "subcultures" can be distinguished - classical behaviorism with Clark Hull as the leading figure, and purposive or functional behaviorism, inaugurated chiefly by Edward Tolman - they can be put together in this context since the functionalism of the latter alter-

native appears ecologically invalid, systematic environmental sampling not being carried out other than through inferences based on empathy (Tolman, 1959, e.g. pp. 147-148). So far as one can tell from their published reports, the overwhelming majority of researchers in this camp never relate the behavior of their experimental animals to their adaptive consequences in nature nor bother to investigate the natural response repertoire of these animals nor explore the ontogenesis of organism/environment relationships prior to experimental manipulation.

The forerunners of modern ethology (e.g. L. Morgan, O. Heinroth, J.S. Huxley and H.S. Jennings) as well as Lorenz (1939) and later Tinbergen (1951), whose early theorizing were the starting-points for the development of todays European ethology, all emphasized innate determinants of behavior (conceptualized as e.g. instincts, innate releasing mechanisms and fixed action patterns) and the qualitative aspects of significant stimuli. Dichotomizing nature and nurture as two separate and distinguishable agents on individual development, with an emphasis on the impact of the former, they formed a sharp contrast to the corresponding American research on animal behavior. Developing independently, these two schools did not confront each other until the 50's when Lehrman (1953) heavily attacked the Lorenzian approach, his main point being that dichotomizing genetic and environmental influences leads to an underestimation of the impact of early, especially prenatal, experiences. Efforts should be directed towards tracing the interacting processes behind the development of behavior patterns, not towards separating reactions as innate or learned. The publication of this article marked the beginning of widespread ciriticism toward what was called Lorenzian ethology, particularly by American researchers. The concept of an innate releasing mechanism, activated by sign stimuli was particularly found fault with. This may be illustrated by the debate

on the presumed innate tendency in certain birds to take cover at the sight of a hawk-shaped figure (Lorenz, 1939; Hirsch, Lindley & Tolman, 1955; Tinbergen, 1957; Melzack, 1961; Schleidt, 1961; Green, Green & Carr, 1966).

There are two main assumptions that apparently are accepted by the learning theorists. (1) All CS - CR relations as well as all combinations of operants and reinforcers are equally associable, and (2) the development of CS - CR and operant - reinforcer relations are governed only by quantitative characteristics of the stimuli and reinforcers involved and the modes of their presentation. It is easy to understand that adherents of such beliefs reacted strongly against the Lorenzian approach which coupled an imprecise methodology with an emphasis on innate dispositions and qualitative stimulus filtering.

These quantitative assumptions held by learning theorists, appear to be inconsistent with the fact based on massive field observations of higher organisms, that the response to a specific stimulus is governed by its significance and depending on the context in which it occurs. Since, for instance, some, but not all,stimuli of very low intensity are biologically significant for a particular species in a particular situation (e.g. sounds of low amplitude to a hunting owl), stimulus quantity seems subordinate to stimulus significance. Likewise, contextual aspects are not easily amendable to quantification. Since, however, quantitative regulation of S - R relations undoubtedly is of great significance in systematic designs with artificially tied variables, i.e. a composition of variables that is unlikely to appear in a natural setting, the challenge is to find out whether the quantitative regulation established in the laboratories can be translated to the qualitative and contextual regulation that is evident when the behavior of the organism is observed from a functional perspective.

In the light of the cursory historical survey presented above, it is interesting to note that recently several authors have pointed out that many of the inconsistent results obtained by learning theorists can be attributed to the fact that the experimental animals are variously "prepared", through their evolutionary history, to establish different S - R relations. Seligman (1970) makes a distinction between S - R relations for which the subjects are prepared, un-prepared or contra-prepared, and Bolles (1970) argues that the conflicting results obtained in the area of avoidance learning is due to the fact that innate species-specific defense reactions of the subjects have not been considered. He cites numerous studies where such defense reactions are persistently elicited after only a few reinforcements while other (un-prepared or contra-prepared) operants need massive reinforcement to meet the same criterion of response frequency. Evidently, the critique that once originated from researchers in the field of learning theory now can be redirected. Neither "innate" nor "prepared" are concepts with explanatory value as long as the ontogenetic development of the presumed innate or prepared response is not traced. To achieve this end, the process-dominated field of learning theory must be supplemented with structural concepts (cf. Doyle, 1971).

The present author consider the only valid starting-point for studies of animal behavior - irrespective of whether the setting and the strategy of the study is laboratorial or naturalistic - to be an analysis of the ecological and functional aspects of the response-pattern investigated. This opinion is based on the rather uncontroversial datum that each behavior-pattern has functional consequences and has evolved as a response to specific environmental demands. In fact, a given behavior and the environment to which it is adapted, constitute components of a Gestalt, which makes analysis of an isolated part of very limited value. This credo coincides with and is supported by the theoretical and methodological opinions of Brunswik (e.g. 1955a

and b) as comprehended by the present author. Brunswik emphasized the importance of analyzing the relationship between the environment and the organism in order to achieve a basis for an understanding of the functional properties (achievements)of the behavior of the organism.

Indeed, the environment of the organism shall be studied as thoroughly as the organism itself to obtain results of ecological validity. He pointed out the limitations of the classical systematic design where, ideally, all but one or a few variables, are held constant. This strategy almost inevitably leads to the organism being studied in atypical contexts with artificial tying of variables and, hence, to results that are difficult to generalize. A representative design, on the other hand, involves variables that are chosen by their biological relevance and in a composition that is ecologically representative. Such a design allows functional conclusions to be drawn from the authentic, "probabilistic" behavior that is exhibited by the subjects. The "probabilistic", i.e. not totally predictable, behavior displayed by an organism in an ecologically valid context is due to the "semi-chaotic" nature of such a context, where specific cues convey information of differing significance depending on the preceding experience of the organism, the state of the organism, and the ever-changing context in which the cue is embedded. Furthermore, all factors relevant for a correct "decision" by the organism, are not accessible to it. Thus, a particular behavior-pattern cannot be more than partly understood or explained as studied by systematic designs, and even less so if only characterized by the physiological mediation mechanisms involved in the S - R transformation.

These opinions do not abolish the use of systematic designs or deny lawfulness on levels of higher complexity ("God does not gamble"; Brunswik, 1955b, p. 236). It follows that e.g. physiological studies are relevant when subordinated to a functional perspective. The probabilistic functionalism is

not hostile to reductionism, but "in order to reduce, we must know what to reduce" (Brunswik, ibid., p. 237).

It is the opinion of the present author, again not original, at least as a proclamation, that an alternating application of systematic and representative designs (which obviously are not possible to sharply delimit from each other) is the optimal strategy, on condition that the first step consists of a descriptive account of the behavioral and ecological environment in which the response-pattern is embedded.

Regarding the probabilistic behavior of organisms, it seems possible to define a gradient of behavior-patterns that are more or less probabilistic, i.e. that are either more governed by situational circumstances (less probabilistic) or primarily "set" to be adaptive in an average environment (more probabilistic). The existence of reactions that are less susceptible to modification by experience points to the existence of corresponding stable environmental patterns and underlines the necessity of ecological sampling in behavioral research. It can be predicted that the more variable (less predictable) the relevant aspects of an organism's environment, the less probabilistic is its behavior. This is because it is forced to respond to the actual and unique situation confronting it rather than to a situation that has much in common with earlier, similar situations. The more predictable the environment, the less is the need for a unique reaction and the more adaptive is a probabilistic response. Evidently, however, there is no higher organism that is capable of perceiving all aspects of its environment that are relevant for a "correct" response (which maximizes the chances for survival) to be displayed in the time accessible for decision. Furthermore, the task of displaying a "correct" response is complicated by the fact that most responses have both negative and positive consequences from a survival point of view, (Tinbergen, 1965).

Accordingly, all behavior has a gambling character due both to limitations in the perceiving and processing powers of the responding organism and to the inherent complexity of its environment.

Area of investigation

It is an old datum in studies of animal and human behavior that a response that is repeatedly elicited by the same stimulus progressively wanes if not reinforced. If effects of effector-fatigue, receptor-adaptation and maturation are excluded, this type of response-decrement has been alternately labeled habituation and extinction.

The concept of extinction is traditionally applied to the decrement of a conditioned response, aspects of the waning process being related to the parameters of conditioning. The responses used in most studies of extinction are selected only for convenience and the methodology applied is often highly sophisticated.

The concept of habituation has more often been confined to the decrement of responses without a known history of conditioning, typically species-specific, "natural" responses, e.g. reactions to predators, rivals and food. The methodology is adjusted to the nature of the response studied, habituation of aggressive responses, for example, being investigated in adjacent territorial cichlid males (Peeke, Herz & Gallagher, 1971). Although primarily process-oriented, functional aspects are often referred to but in a superficial and vague manner by merely pointing out that response-waning to an irrelevant stimulus is adaptive.

In 1966, after reviewing both behavioral and physiological studies, Thomson and Spencer suggested an operational definition of habituation consisting of nine criteria. These included

process characteristics and related the phenomenon to quantitative aspects of the stimulus and to the modes of stimulus-administration. The similarities between habituation and extinction were emphasized and it was suggested that common neuronal mechanisms existed. Recently, Groves and Thomson (1970), have substantiated a simple dual-process model where the behavioral characteristics of habituation are correlated with physiological activity on the neuronal level in partly localized substrates. Two independent processes, one decremental (habituation) taking place in the S - R pathway, ("however circuitous, redundant and variable") and one incremental (sensitization) localized in those regions and systems that determines the general level of responsiveness of the organism, are assumed to develop independently on repeated stimulus presentations and interact to produce the behavioral outcome. The incremental process is related to and governed by the "state" of the organism, ("merely a short-hand summary of the many factors that influence the general excitability or tendency to make responses of the organism") a concept that seems to be of doubtful explanatory value since the causes of differences in "state" are not integrated in the model.

Interpreting the results of functionally oriented studies, quantitative aspects of the response-eliciting stimulus and its presentation seem to be of less importance than its meaningfulness to the organism, a point that was first experimentally supported by Lorenz (1939), studying escape reactions to an alternative goose/hawk model, and later repeated by Thorpe (1963) with reference to further studies of anti-predator responses. Hinde (1954a) found that, with the Chaffinch Fringilla coelebs, owls are particularly effective in evoking the mobbing response, although any strange bird might evoke it at some strength. Nice and ter Pelkwijk (1941) made similar observations on young Song Sparrows Melospiza melodia and Rouse (1905) reported that when pigeons were exposed to what

he classified as significant or meaningless sounds, they remained sensitive to the significant ones and habituated to the meaningless ones, irrespective of the stimulus quantity employed.

As suggested by these authors, a varying, genetically coded "preparedness", seems to govern the rate of habituation to significant stimuli, an assumption that is congruent with Orr's observation (1945) that Galapagos finches which have been isolated for centuries with no predatory land mammals or hawks in the environment,still exhibit an alarm reaction to hawks. Although difficult to interpret, the results of Curio's studies (1969) with the same species of birds, are also analyzed in terms of the evolution under selection pressure of an ability to recognize avian predators and to display slow habituation to such stimuli.

In contrast to these interpretations in terms of innate ability to select and respond to stimuli by their significance, this variable being qualitatively assessed (hawk-shaped figure, owl-characteristics, etc.), a number of authors have argued that the effects of such significant stimuli can be explained in terms of their novelty (Schleidt, 1961; Melzack, 1961; Schaller & Emlen, 1962) and high intensity (Schleidt, 1961; Schneirla, 1965).

Finally a puzzling observation that has been made when anti-predator responses have been studied in experimental settings, is the development of an enduring response decrement (Hinde, 1954b; Melzack, 1961), a reaction that can not be expected to occur in nature due to its obvious dysgenic consequences (cf. Rydén, 1970). This observation indicate that the investigated species are able to modify basic response tendencies to specific contexts and, consequently, that habituation is governed in a more complex way than can be understood by considering

isolated stimulus characteristics only. It has been suggested by Lorenz (1965) that the stereotypy of the experimental setting is the decisive factor. Hinde (1954b) tried to break this stereotypy by moving around the stimulus (a stuffed owl) but did not manage to interrupt habituation in this way. Apparently, the reactions of his subjects (chaffinches) were governed by Gestalt-characteristics of the test situation that remained constant in spite of his alterations.

In summary, variations in the process of response-waning upon repeated stimulus-presentations has been interpreted as due to 1) solely quantitative aspects of the response-eliciting stimulus and the modes of its presentation, 2) the meaningfulness or functional significance of the stimulus, assessed qualitatively, in combination with contextual characteristics, and 3) the interaction of two processes on the neuronal level of which one (incremental) is governed by all factors that regulate the organism's general tendency to respond.The effects of this last inferred excitatory state evidently has room for a host of concepts with structural implications, like performed or innate response-patterns, stimulus-selective mechanisms etc.

Studying habituation on the neuronal level is doomed to bring about very limited achievements towards an explanation of this phenomenon if a particular stimulus is responded to differently in different contexts and depending on the prior experience of the organism. On neural levels, where convergence of information occurs from all sensory systems and from stored past experience, more complex correlations can be made between physiological and behavioral data (cf. Groves & Lynch, 1972). But since knowledge is quite limited on how phylogenetic and ontogenetic experience as well as the effects of motivational and environmental variables are represented physiologically and interact to produce observed behavior, it seems more practical to increase our knowledge on how functional and onto-

genetic factors influence the behavioral process; and, from a platform of such knowledge, design physiological studies where these factors are represented as independent variables.

Analogously, the quality/quantity issue may be investigated when subordinated to a functional perspective, provided that unambiguous functional predictions can be derived.

This opinion, that a functional orientation is underrepresented in studies of habituation, has quite recently been emphasized by both behavioral researchers (Petrinovich, 1973) and physiologists (Worden, 1973).

The studies to be summarized below were designed to contribute to an understanding of which factors influence the process of habituation or extinction. Rate of response-waning was regarded as one aspect of response-strength, which also can be assessed by supplementary measures. Applying these measures, the effects of varying the biological significance of the response-eliciting stimulus as well as the impact of ontogenetic experience on these measures of response-strength were investigated. The questions raised were: (1) If a species-specific, adaptively "important", response is repeatedly elicited by stimuli of varying biological significance, is the rate of response-waning correlated with the significance of the stimulus? (2) If such a correlation can be demonstrated, are differences in stimulus-significance translatable into differences in stimulus quantity? (3) Is it possible to trace ontogenetic influences that govern the development of a varying responsiveness to the employed stimuli? (4) Is it possible to relate rate of habituation to other ractions to a given stimulus, thereby including rate of habituation in a behavioral unit that is functionally related to a particular stimulus or class of stimuli?

S t r a t e g y

Response selected

Since species-specific anti-predator responses can be assumed to be of high adaptive significance and since such responses are elicited by an array of stimuli, one such response, cessation of begging in young birds, was selected for investigation and studied on Great Tit nestlings Parus major. This response is suitable since it has an easily assessed un-manipulated strength and frequency against which reliable estimates of the effects of the employed stimuli can be obtained.

The chicks of this altricial passerine are, at hatching, blind, naked and completely dependent on their parents due to their undifferentiated stage of development and have a very limited repertoire of gross responses until a few days before exodus. Their growth rate is remarkable, their weight increasing linearly from about 1,5 grams at hatching to about 19 grams at 14 days of age (van Balen, 1973). The brood is visited 400-500 times per day, making 30-50 visits per nestling depending on the size of the brood (Gibb, 1950). At each single visit, all nestlings beg vigorously until around 30-60 secs after the feeding bird has left, the duration of begging being dependent on the state of satiation of the brood. During the first days, begging is primarily activated by tactual stimuli and its cessation does not seem to be governed by external stimulation. As can be predicted from the visually isolated position of the nest, auditory stimuli progressively dominate the regulation of the begging response and, at least from about 12 days of age, parental alarm-notes, as well as sudden noises, effectively lead to cessation of begging. When the nestling is about 14 days old, the cease-begging response can be observed to vary in duration depending on which stimulus elicited it. Any sudden, new and/or intensive stimulus evokes a transient cease-begging response, while parental alarm-notes eleicit a response of longer duration.

Since observations of juvenile Great Tits of varying age indicate that suppression of movements and a crouched posture is increasingly apparent in combination with cessation of begging as a response to parental alarm-notes, it has been concluded that the simple cease-begging response of the nestling is the first representation of a gradually developing response which finally is established as the freezing response of the adult bird which is elicited by stimuli indicating acute danger, primarily the ´seet´ alarm-note and the sight of a flying Sparrowhawk Accipiter nisus (Hinde, 1952; Marler, 1956).

Adaptive significance

As summarized by Nice (1957), the nestlings of hole-nesting, altricial birds suffer less from predation before exodus than open-nesters, the mean percentage of nestlings surviving to exodus being 86 and 72 for the first and second category, respectively (eggs that never hatch not included). The corresponding figures from four studies of the Great Tit are 86, 71, 95 and 80 % (Nice, 1957, p. 308). In one project where the breeding success in Great Tit populations has been monitored over several years in the area from which the birds in the present studies originate, and average mortality of less than 5 % until exodus has been assessed. In this case the mortality is undoubtedly primarily caused by starvation (Källander, unpublished data). Perrins (1965) showed that a larger proportion of Great Tit nestlings was taken by weasels Mustela nivalis from large than from small broods, and from late compared to early broods. The begging calls emitted by the young obviously guided the weasels to the nests. In further studies on the predation by weasels, this result has not been consistently repeated. Since the availability of alternative preys for this predator very well may vary independently of the factors that govern the size of broods and number of late broods, Perrin's finding may not be generally valid (Källander, pers. comm.).

Regarding juvenile survival (after exodus), only a small proportion (probably on average about 25%; Lack, 1966, pp. 60-61) survives to enter the breeding population on the following spring. Opinions differ on when the heaviest losses occur and whether starvation, predation or predation as affected by starvation is the main mortality factor (for reviews, see Lack, 1966, cp. 3 and 4, and von Hartman, 1971). Although the Great Tit is a thouroughly investigated species, methodological difficulties have hindered an elucidation of the fates of the young Great Tits after they have left the nest.

It has been shown by Tinbergen (1946), however, that the toll paid to Sparrowhawks by the Great Tit can be substantial. In one individual case this even included nestlings of this and other hole-nesting species (Tinbergen, 1946, pp. 97-98).

Since the anti-predator reactions of the Great Tit presumably have developed under a higher predation-pressure than now prevails, and, furthermore, since each behavior that only marginally increases the individual's chance for survival tends to be increasingly represented in the population, it can be assumed that cessation of begging, as a means of avoiding detection by predators, is a response of adaptive significance for both nestling and juvenile Great Tits. Predictions about relative response-strength, in this case duration of the cease-begging response when elicited by stimuli of varying significance, can be derived and, if verified, constitute a frame of reference or starting-point for studies of the ontogenesis, proximal causation, and physiological mediation of the observed behavior.

Experimental designs

The basic method used to study the effects of the employed stimuli was to measure the duration of a brood's begging response after feeding, accomplished either by the parents in the natural

environment or by the author in the laboratory. A measure of response-strength was obtained by comparing the duration of begging when a stimulus had been administered immediately after feeding versus when it had not. In the laboratory experiments, the nestlings were fed at ten minutes intervals, the amount of food calculated to "calibrate" the begging duration after feeding at a level optimal for the experiment. To obtain more data, the nestlings in each brood were divided in pairs and each pair was tested separately. Since the mode of stimulus administration was equal for all groups, the effects of the employed stimuli were assessed by inter-group comparisons. Each stimulus and blind trials were presented in ABBA-sequences to avoid position-effects.

In the field experiment two stimuli were presented to each brood alternately at every second feeding, each stimulus thus being administered at every fourth feeding. The effects of the stimuli thus were obtained by intra-group comparisons, since the irregularities of the parents' feeding made inter-group comparisons difficult. This irregularity also made position effects less probable.

To obtain supplementary measures of response-strength, the contrary response, begging, was conditioned to the same stimuli and later extinguished. In this way, the two dominant responses of the nestlings were utilized.

To facilitate predictions on a functional level, the following auditory stimuli from the habitats of the Great Tit were selected (an acoustic analysis of these sounds are presented in (I)): (1) The ´seet´alarm-note of the Great Tit which is elicited in situations of acute danger (p. 14);

(2) (1) replayed at half speed. This stimulus sounds like a flute-note and contrasts very sharply with any natural sound

in the habitats of the Great Tit. It is thus both new and unsignificant;

(3) The ´seet´-call of the Blackbird Turdus merula recorded from a wild, male bird in a threatening context. According to Messmer & Messmer (1956) and Heyder (1967), it is also a contact note in the beginning of pair formation and furthermore is "used as the expression of desire" (Messmer & Messmer, 1965). Marler (1955) considers this call as functionally analogous with the ´seet´-call described above. Snow (1958, p. 58) points out that it is also used in less threatening situations. Moreover, he distinguishes it from a similar, slightly more high-pitched ´see´, which occurs in combination with aggressive behavior. Tretzel (1966) has published sonagrams of this note, uttered by a male Blackbird in a slightly threatening situation and by both members of a pair during mating, which are indistinguisable from each other and from the recording employed here. A possible "smallest common denominator" for the contexts where this sound is emitted may be a conflict between tendencies to flee and to attack.-It is thus not settled whether the call used in this investigation, besides being uttered in dangerous situations, is synonymous with or slightly different from a contact note and/or an aggressive note of the same species;

(4) and (5) Song-strophes of the Tree-creeper Certhia familiaris and the Robin Erithacus rubecula both of which contain the high frequenties that characterizes the ´seet´-call;

(6) A song strophe of the Great Tit.-These stimuli were selected to make it possible to evaluate the effects of stimulus significance and, if such effects were found, to gain some insight into which quantitative characteristics of a stimulus that are associated with its significance.

If the experiential antecedents of the investigated reactions to these stimuli were to be traced, the auditory environment of the Great Tit nestling had to be sampled. The frequency of occurence of the employed auditory stimuli were initially assessed by unsystematic field-observations. To obtain more reliable estimates, a rather thorough registration of the sounds occurring at eight Great Tit broods of different ages were made during some 37 hours (IV).

The employed stimuli were played back by a tape recorder, in the field experiment through loudspeakers attached close to the nesting-boxes. The intensity of the sounds were subjectively adjusted to correspond to a natural stimulus. In the introductory field experiment, the reactions of the nestlings were registered through a microphone, attached to the ceiling of the nesting-box. In the field, all observations were made from a hide, situated 5-10 metres from the nest.

Most of the nestlings were tested at 16-18 days of age. The brood leaves the nest at the age of about 19 days (17-21 days; Gibb, 1950). Since the begging-call of the nestlings become progressively louder during the nest period, its potential to act as a cue for mammalian predators simultaneously increases and, consequently, the adaptive value of the cease-begging response becomes gradually higher. The choice of this age-group was also based on the assumption that the observed reactions characterize newly fledged nestlings that also are decimated by aerial predators.

Summary of experiments

In the first experiment, the reactions of 16-18 days old, wild nestlings were tested in the field to minimize the possibly distorting effects of an artificial setting. The stimuli were replayed at the nesting-boxes while the chicks were normally fed by their parents (I). - As the next step, nestlings of the same

age, taken either from wild broods and tested after one day in captivity or raised in the laboratory from 8-9 days of age, were tested in the laboratory (III). By this procedure, the generality of the results obtained could be evaluated by comparing the responses of the wild-captured broods with the previously tested, wild nestlings. Simultaneously, the impact of normal auditory experience during 7-9 days before the test, on the reactions studied, could be estimated. - Subsequently, the reactions of 10 days old chicks, obtained from wild broods, at 8 days of age, were tested in order to trace the development on the studied reactions (II). - Finally, the modifiability of these reactions were tested by subjecting three broods to a massive exposure of the main stimulus employed, the ´seet´-call of the species, in one of three contexts that connected the stimulus to either feeding, alarming situations or to a neutral context. The broods were subsequently tested in the laboratory when 16-18 days old and their reactions compared to the earlier studied wild-captured and laboratory-raised birds of the same age (IV).

Results and discussion

Estimating the effects of stimuli of varying significance in a natural context (I).

Stimuli (1) - (5), described above, were replayed to 32 broods of 16-18 days old chicks at their nests. Two stimuli were alternately replayed with a blind trials interspersed between each stimulus administration. The responses were grouped in three categories: positive (immediate silence); weak (weak and/or sparse begging) and negative (no difference in begging duration as compared to the preceding blind trial). It was found that replayed song-strophes of the Tree-creeper and the Robin and the Great Tit ´seet´-call, replayed with half speed, only temporarily or not at all affected the duration of begging while the two ´seet´-calls employed produced persistent cease-begging responses, the Great Tit ´seet´-call having the strong-

est effect. By relating the duration of begging after feeding to number of cease-begging responses elicited during habituation, it was shown that a high intensity of begging coincided with a faster habituation of the response than did a lower intensity of begging. Additionally, the effects of varying the stimulus quantity were tested by (1) replaying the two ´seet´-calls once instead of three times as in the preceding series; and (2) after habituation had taken place, by replaying the stimulus at a much higher intensity in an effort to dishabituate the response. It turned out that replaying the ´seet´-calls once instead of three times did not have any, or at most a doubtful, response-decreasing effect. On the other hand, drastically raising the amplitude of the stimuli produced a return of a relatively persistent cease-begging response for two broods which were subjected to the Great Tit ´seet´- call and the elicitation of this response in two other broods which did not respond to the replaying of this call at the normal amplitude. This reaction was less obvious for the Blackbird ´seet´-call and did not occur at all with the Tree-creeper and Robin song-strophes. Finally, some evidence was found for Groves and Thomson's (1970) conception of behavioral habituation as produced by two independent processes, habituation and sensitization, in that the process of rehabituation did not replicate the preceding habituation but contained more weak and negative responses before the criterion of habituation was attained. This would seem to indicate that behavioral habituation was governed by a superimposed sensitization while physiological habituation proceeded unaffected. Thus, the relative influence of these two processes on the behavioral outcome changed to a greater dominance of habituation.

Since the higher effectiveness of significant as compared to neutral or insignificant stimuli could not be explained as due to their novelty or by hypothesizing a differential prior reinforcement, it was concluded that activity in a stimulus-

selective mechanism, evolved through phylogenetic adaptation, somehow governed the course of habituation of the cease-begging response by means of a response-sensitization or by affecting the state of the organism.

It may be noted that "Lorenzian" interpretations, like this one, lie near at hand when the effects of normal early experience have not been investigated through a manipulation of this experience. Such an interpretation, however, is not invalidated if it is demonstrated that early auditory experience governs the reactions to calls encountered later in the ontogenesis. It is rather substantiated, if it can be shown that the organism is "biased" to establish S - R relations that are of adaptive value.

A laboratory study of the reactions of 10 days old chicks to a positive (Great Tit song), a neutral (Tree-creeper song) and a negative (the ´seet´-call) stimulus (II).

In this study, the chicks were first subjected to the stimuli replayed immediately after feeding. In contrast to the reactions of older chicks in the previous study, they did not react by cease-begging or a decreased begging-duration. - Subsequently, the same stimuli were replayed 10 secs before each feeding in an effort to connect the contrary response, begging, to these stimuli. Now, it turned out that begging was much more difficult to associate with the ´seet´- call compared to GT- and TC-song. In three pairs of chicks, presented the ´seet´-call, 12, 14 and 17 trials preceded the established criterion of conditioning, and another three pairs never reached this criterion (the experiment was interrupted after 34, 39 and 39 trials). This difference between stimuli is notable since it is indicated by the few trials that were neccessary to connect the begging response to TC-song (2,5 and 5), that the chicks easily adapt to new experiences, at least in this artificial context. Although no differences in regression rates were found

between stimuli when the established CS-CR relations were finally extinguished, the GT-song elicited a higher initial duration of begging than did TC-song. The weak evidence available for the ´seet´-call indicated a very fast extinction of the begging response when associated with this stimulus.

Following Schneirla (1965), the observed reactions were grouped on an withdrawal-approach dimension with cease of begging and begging at the respective pole. It was concluded that, while begging was not silenced by the ´seet´-call, reactions analogous with those of older chicks could still be identified when an approach response, begging, was connected to this stimulus. Evidently, already at 10 days of age, GT chicks exhibit a less approach to the ´seet´-call than to control stimuli. This differentiating ability would not be apparent from their spontaneous behaviour in a natural context but can be established by introducing a situation with greater differentiating power that is not encountered in nature. There are two alternative ways to interpret the different reactions to the ´seet´-call displayed by 10 days old as compared to 16-18 days old chicks. (1) Some experiential factor that reinforces withdrawal reactions to the ´seet´-call has strengthened this tendency in the older age-group. (2) Some situational factor has the effect that the begging response is stronger motivated in the younger age-group. - The last alternative was suggested (III, p. 18 ff.) to be supported by the fact that, because of a higher metabolic rate (van Balen, 1973), the younger chicks end up in a state of deprivation sooner and hence can be expected to pay less attention to stimuli which are not food-related (cf. I, p. 12.). It was furthermore hypothesized that, whatever factors had produced the observed stimulus-selectivity towards auditory stimuli, would be less firmly established in the younger chicks since they recently had passed an ontogenetic level where they primarily react to tactile stimulation. - One cannot rule out the possi-

bility that some experiential influence might have strengthened the cease-begging response in the older chicks but testing this proposition would include; (1) comparisons between laboratory-raised and wild-captured chicks of the same age and, (2) a demonstration of the modifiability of the observed reactions by experiences that might occur in nature.

The dependence on normal auditory experience for appropriate later reactions to the ´seet´-call. A comparison of 16-18 days old laboratory-raised and wild-captured nestlings (III). In this study, 26 nestlings were obtained from wild broods when 8-9 days old and raised artificially until 16-18 days old. Another 18 nestlings were captured the day before this age and tested the following day. The two groups of chicks were compared with respect to (1) rate of habituation of the cease-begging response when elicited by either GT-song, TC-song or the ´seet´-call; (2) resistance to conditioning of the begging response to the same stimuli; (3) rate of extinction of the begging response when thus conditioned. In the habituation test, neither the laboratory-raised (l-r), nor the wild-captured (w-c) birds responded by cease-begging to GT- or TC-song, although an initial suppression of begging was exhibited by the w-c pairs. The ´seet´-call, on the other hand, elicited cessation of begging and suppressed begging during about 10 test trials in both groups. In the following conditioning test, the begging response was connected to TC- and GT-song after 0-3 trials in both groups while it took 16, 18 and 19 trials for the three w-c pairs to establish the ´seet´-call as a CS, eliciting begging as a CR. Since the corresponding number of trials for six l-r pairs were 7, 10, 11, 12, 12 and 14, the artificially raised chicks displayed a weaker withdrawal to the ´seet´-call than did the naturally raised nestlings. - During extinction, the w-c nestlings displayed differential regression rates between stimuli in that the begging response waned more than twice as fast

when conditioned to the ´seet´-call as compared to GT-song, TC-song occupying an intermediate position. No overall differences were found in the 1-r pairs but GT-song tended to elicit a more extinction-resistant begging response than did TC-song. When compared to 10 days old chicks, the 1-r birds in this study exhibited a stronger withdrawal to the ´seet´-call without having been exposed neither to this note nor to any other parental calls. The w-c birds, on the other hand, showed an even stronger withdrawal to the alarm-note. - The conclusion to be drawn is that prior experience of the ´seet´-call is not a neccessary antecedent of the strong withdrawal reactions elicited by this call in 16-18 days old nestlings. However, some experiential factor apparently is able to strengthen this behavior.

Two characteristics of the ´seet´-call were hypothesized to account for its ability to activate withdrawal, viz., its novelty and intensity.

The arousing effect of stimulus-novelty is well proven and has been put forward as an explanation for the generally inappropriately strong reactions shown by animals that have been raised in isolation. According to this interpretation, this is caused by their lack of opportunity, compared to non-deprived individuals, to habituate to normal environmental stimuli (Fuller, 1967). As already pointed out (p. 10), several authors have explained the stronger reactions elicited by predators as an effect of the relative novelty of such stimuli. Similarly, it has been argued that flying predators, especially when swooping towards the prey, present a more intensive stimulation due to the relation between speed and size that characterizes them (Mc Niven, 1960; Müller, 1961; Schleidt, 1961). These conclusions, although concerning visual stimuli, seem applicable to our results. The ´seet´-call had presumably never, or at most rarely, been encountered by the 1-r nestlings before the test. Acoustically,

it is also very different from the begging-call of the chicks which is supposed to form an auditory base-line since it had been the completly dominating element of their prior auditory experience. The begging-call covers a wide frequency-range while the ´seet´-call is a very high-pitched sound.

As for the intensity of the ´seet´-call, it may superficially be classified as a stimulus of comparatively low intensity, especially compared to the begging-call of the nestling and its peers in combination. To a human ear, it has a weak but piercing quality, probably because it is composed of a narrow range of very high frequencies (8.4 - 7.8 KHz). The human ear has a relatively low sensitivity to these frequencies. On the other hand, the high concentration of energy on a narrow spectrum of frequencies brings about a very concentrated perceptual load, and, speculatively, the more so with a high-frequency sound, since the short wawe-lengths presumably causes more processing per time unit. It may for these reasons be classified as (physiologically) more intense than a sound of the same physical intensity (in terms of W/m^2) that is composed of lower and more dispersed frequencies. Since the auditory threshold curves that are known for small birds (e.g. the Bullfinch Pyrrhula pyrrhula; Schwartzkopf, 1968), are very similar to that of man, this argument would be applicable to the Great Tit as well.

As already concluded, (I, p. 15), sheer novelty of a stimulus is not sufficient to cause prolonged responsiveness. Neither, for that matter, is intensity as witnessed by the lack of effect when the amplitude of neutral or meaningless stimuli were drastically raised in the introductory field study (p. 20). It follows from the reasoning above, however, that the ´seet´-call is not only a novel stimulus and a relatively intense one as well, but it is intensive in a new way. It thereby deviates from most auditory stimuli experienced by the nestlings

prior to the test.

Alterations of withdrawal-reactions to the ´seet´-call. The modification of a "spontaneous" response in a combined field- and laboratory study (IV).

In the preceding investigations, the ´seet´-call not only elicited an initially stronger responsiveness than did control stimuli but this responsiveness was also quite persistent. The ´seet´-call did not become neutralized or attain a positive value in the same rate or to the same degree as did control stimuli. Evidently, the chicks seemed negatively "biased" towards this note even before the age of about 10 days when testing first took place - a tendency that was quite resistant to modification. At the same time this tendency is strengthened during individual development in the nest between ca. 10 and 16-18 days of age.- The next study was designed to investigate the background of these seemingly contradictory characteristics of responses activated by the ´seet´-call.

Three broods were subjected to about two hours of replayings of the ´seet´-call in their nesting-boxes during each of four consecutive days when they were 11-14 days old. The replayings were made in one of three alternative contexts for each brood: (1) just before feedings, (2) when the parents were not present, and (3) in connection with the display of a stuffed Sparrowhawk or together with attacks on the nesting-box and a temporary removal of one chick - measures that caused the utmost alarm in the adult birds. These procedures were carried out in an effort to (1) connect the begging-response of the chicks to the alarm-note and thus reverse the spontaneous response to this stimulus; (2) investigate the effects of massive earlier experience in a neutral context on later reactions to the ´seet´-call, which, after this treatment, would no longer be a novel stimulus to the chicks; (3) study the effects of

experiences that, although probably uncommon, may occur in nature. - To obtain an estimate of the auditory experience normally accumulated by GT nestlings, some 37 hours were dedicated to registering the auditory environment of eight GT broods. - After about 1 1/2 days, the reactions of six chicks from each brood were investigated by the same tests applied earlier (II and III).

In the habituation test, marked inter-group differences were shown in that no cease-begging responses were recorded in the group with a prior positive experience ('seet'-call associated with feeding). Thirty-three such responses were displayed by the three pairs with negative experience ('seet'-call in alarming situations). The neutral group ('seet'-call between feedings) occupied an intermediate position, exhibiting, in all, 16 cease-begging responses, a number equal to that recorded in the earlier tested wild-captured nestlings (natural group). - In the conditioning test, inter-group positions were generally unchanged but became less conspicious. Furthermore, substantially more negative trials were recorded in the natural than in the neutral group in this test. - During extinction of the previously conditioned begging-response, the flatest regressions were found in the positive group; there were small differences between the neutral and the natural groups and the scanty evidence available for the negative group indicated a very steep regression.

Observation of GT broods of varying ages indicated substantial interbrood differences, both quantitatively and qualitatively, with regard to the auditory experience accumulated by the nestlings from different broods before exodus. Hence, the earlier derived conclusion that prior experience of the 'seet'-call is not neccessary to develop appropriate reactions to this stimulus was supported. Since the behavior of the neutral group showed that extensive experience with this call per se

does not weaken the tendency to withdraw from it, it was concluded that this tendency is based on an early developed, habitual preference for stimuli with opposite qualities. It was suggested that this preference partly originates from a massive experience of the begging-call. This call is the only element that is both common to and dominant in the auditory experience of all nestlings. Moreover, it has been thoroughly associated with approach responses at numerous occasions through parental feeding.

This suggestion was derived from Schneirla's theory (1965) that prenatal experiences of proximal stimuli of low frequency, low magnitude and regular timing associated with para-sympathically regulated processes (A-processes) constitute the experiential base for a general tendency in neonatal animals to approach stimuli with these characteristics and to withdraw from stimuli having the opposite qualities. Hence, the reactions to external stimuli would be based on their quantitative, not their qualitative characteristics. Schneirla, (ibid. pp. 21 & 31-32) suggests that late prenatal and early postnatal experiences of mainly auditory stimuli, influence the nature of these preferences. This suggestion is supported by the finding, in several precocial species of birds, that exposure to normal auditory stimulation before hatching (corresponding to some portion of the pre-exodus phase in altricial species), is essential to the development of species-specific auditory perception (see Gottlieb, 1968 for summary and review). It has, furthermore, been shown by Dimond (1968) that the level of visual stimulation prior to hatching governs the later preference level in chicks.

Since, with respect to birds, quite extensive interactions take place between the embryo in late phases and it's "extra-shell" environment, at least in precocial species, it appears difficult to differentiate between the relative effects of pro-

ximal (proprioceptive and kinestethic) and later (late prenatal and early postnatal) distal stimulation. Referring to experiments by Lehrman (1953) and Schaller & Emlen (1961), where it was shown that gaping by Red-winged Blackbirds Agelaius phoeniceus and Grackles Quiasculus quiascula initially is elicited by a wide range of visual stimuli and later only by the features of the parents, Schneirla concludes that .. "In these cases, a learning reinforced by A(pproach)-processes as well as by feeding is indicated" (1965, p. 21). Thus, an interaction is assumed between the viscerally based A-processes and extrinsic reinforcement, in this case brought about by the parents. The further assumption, made by the present author, that the acoustic characteristics of the concurrent calls emitted by the chicks are associated with approach responses, then appears congruent with Schneirla's theory.

It may further be pointed out that withdrawal reactions develop later in ontogenesis than do approach responses, an observation that has been made by many authors for various organisms, and explained by Schneirla (ibid. p. 62), as due to the relative scarcity during embryogenesis of higher quantitative inputs that activate W(ithdrawal)-processes. This condition may strengthen the relation between early approach responses and the concomitant exterior stimulation as a contrast to the later developed avoidance responses and the exterior stimulation of higher intensity that are associated with such responses.

It follows from Schneirla's theory that, if the growing organism is to adapt successfully to its environment, the quantitative characteristics of significant stimuli it encounters should correspond with its disposition to react by approach or withdrawal on the basis of stimulus-quantity. It would be predicted, for example, that stimuli signifying danger must be of relatively high intensity in order to be able to elicit "spon-

taneous" withdrawal. This hypothesis has been applied to explain neonatal animals' avoidance of visual cliffs (Schneirla, 1965, pp. 16-17) and, as already mentioned, hawk-shaped models (ibid. pp. 14-16). In the present case, if it is accepted that exposure to the begging-call influences the "setting" of the GT nestling's quantitative stimulus preferences, it is notable that the ´seet´ alarm-note deviates from this call in terms of frequency and frequency-range, both of which can be assessed in quantitative terms.

If the ´seet´-call is experienced as "unpleasant" by GT-chicks due to its acoustic character, then withdrawal responses to this call would be reinforced by being connected to its cessation and in this way an instrumental conditioning would take place. This might explain the persistence and fast dishabituation of withdrawal responses to the ´seet´-call in the applied tests. It was repeatedly shown, for instance, that, although the ´seet´-call was experienced in more trials in the habituation test than the other stimuli, it nevertheless evoked the highest resistance when the begging response subsequently was conditioned to the same stimuli. This can be interpreted as due to a reinforcement of the cease-begging response in the preceding habituation test that was progressively overshadowed by habituation of this response due to the repeated stimulus-presentations. In an informal experiment with hand-raised GT chicks, it was also shown that, in spite of their begging-response having been thoroughly conditioned to the ´seet´-call, after a pause of two days, the same stimulus had almost entirely lost it's "positive" character to the chicks and only elicited a few begging calls.

The results of the fourth experiment together with the earlier findings led to the conclusion that the reactions of GT-nestlings to the ´seet´-call and stimuli with similar characteristics, in each moment are governed by two separate factors:

(1) A constant tendency to withdraw from such stimuli, the specific response activated being dependent on the situation and the stage of development of the chick. (2) Temporary or context-specific effects of experiences that have decreased or increased this basic tendency to withdraw. An interaction between these two factors was suggested in an attempt to explain the changes in intergroup positions recorded between the habituation test and the conditioning test. Since the criterion to be reached in the habituation test - to cease to withdraw - was less divergent from the presumed basic tendency than the approaching response - begging - that was established in the conditioning test, the prior differing experiences of the groups generally ought to have a greater impact in the habituation test. More specifically, the power of these two tests to differentiate between the groups depended on the size of the difference in withdrawal tendency between these groups in relation to the different criteria to be reached in the tests. The size of this difference, in turn, varied, in the habituation test, with how similar the situation was to the situation in which each of the groups had aquired its prior experience of the ´seet´-call and, in the conditioning test, with the effects that this difference produced when the groups were subjected to the habituation test. This analysis explained the generally decreasing differences between groups in the conditioning test compared to the habituation test and, furthermore, led to the suggestion that the natural group earlier had connected the ´seet´-call with not-feeding. - Finally it was pointed out that this interpretation has to be validated by supplementary experiments, especially those that include groups of chicks subjected to the tests in reversed order.

From a functional perspective, it was considered particularly interesting that it was easier to bring about a decrease than to increase withdrawal from the ´seet´-call. Evidently, the strength of withdrawal that is elicited by the ´seet´-

call is of the same order of magnitude whether the nestlings have had auditory experiences which ordinarily can be expected in nature, or have been subjected to less probable influences that reinforce withdrawal reactions.

Finally, it was suggested that an interaction of a constant tendency to withdraw from stimuli with the characteristics of the ´seet´-call and superimposed transient effects of situation-specific learning would explain the adaptability of the species to stimuli that as a rule are dangerous but irrelevant in certain contexts. A few points were made to illustrate this conclusion.

(1) A very frequent presentation of the ´seet´-call or a hawk-model leads to response-waning. Such frequent presentations, however, probably only occur in experimental settings and in the vicinity of a predators nest - where it is known not to hunt.

(2) As already mentioned (p. 10), responses to alarming stimuli have been observed to wane enduringly in experimental settings, presumably as an effect of the stereotypi of the context. These observations agree with the supposition that a basic tendency to withdraw from such stimuli can be modified as an adaptation to specific situations. This may be illustrated by the differential habituation of anti-predator behavior that is shown to individual predators depending on the context in which they occur, e.g. whether they appear in situations where they can be expected to hunt or not.

(3) The ´seet´-call elicits withdrawal (cessation of begging in young birds and freezing in adults), even if the responding individual does not itself perceive, let alone is hunted by, the predator that caused the call to be emitted by another individual. Still, these reactions are not extinguished. This

is possible to explain if it is presumed that the reactions are reinforced by the disappearance of the ´seet´-call.

(4) It has been shown by Marler (1955) that calls with the characteristics of the ´seet´-alarm note generally signify acute danger. Hence, it would not be dysgenic to habitually respond by withdrawal to all such stimuli irrespective of individual experience of their significance. As earlier mentioned, the Blackbird's ´seet´-note is a problematic case, since it seems to serve several functions and during pair formation and establishing of the territories is extremely abundant. Possibly, some other characteristic of this note that vary in different contexts (e.g. it's patterning), causes a differential response.

C o n c l u d i n g r e m a r k s

Reactions by young Great Tits to natural auditory stimuli

When the audible reactions of GT nestlings were monitored (I) and also when the auditory environment of GT broods of varying ages was recorded (IV), it was repeatedly observed that, at least from 14 days of age, the nestlings responded by vigorous begging to feeding-notes and to song-strophes emitted by the parents, sometimes from a distance of 20-30 metres. Even the common alarm-note ´churr´ elicited begging in hungry broods. Simultaneously, various other bird calls and songs, often emitted close to the nest with considerable intensity (especially the songs and other calls of the Nightingale Luscinia luscinia, the Chaffinch Fringilla coelebs and the Pied Flycatcher Ficedula hypoleuca), were ignored. Thus, a selective responsiveness to natural auditory stimuli develops during the nest-time on the basis of differential reinforcement.

If the rapid establishment of a conditioned begging response elicited by TC-song, demonstrated in both ca. 10 days and 16-18

days old chicks (II and III), is taken as a representative behavior, the nestlings furthermore would have a considerable potential for adaptation to new auditory stimuli. Such a capacity might be predicted on the grounds that the species has an extensive repertoire of calls.

In conclusion, the reactions of young Great Tits to natural auditory stimuli, during the last part of their nest time and when newly fledged, would be governed by: (1) a habitual tendency to withdraw from stimuli with the characteristics of the ´seet´ alarm-note,which tendency may be reinforced merely by the display of this reaction; (2) a tendency to approach and beg as a response to parental feeding notes and song and to ignore calls and songs emitted by other species; and (3) a considerable ability to adapt to the consequences of new auditory experiences.

Habituation versus extinction

If the concepts of habituation and extinction are used with reference to a behavioral process, they can be distinguished - stressing their similarities - by defining habituation as the extinction of an unconditioned response and extinction as habituation of a conditioned response. However, labeling a S - R relation "unconditioned" is, of course, just a way of saying that the factors governing its ontogenesis are unknown. It may very well involve conditioning (Nyström, 1970). However, it can be concluded from investigations of the development of species-specific responses of evident adaptive value, e.g. reactions to dangerous situations (experiments on reactions to visual cliffs and predators or to stimuli announcing predators) or to conspecifics (experiments on imprinting), that the classical concepts within learning theory do not suffice to explain the extraordinarily early, strong and lasting S - R relations that are established. Additional concepts (like exposure learning) have been suggested to explain the emergence

of S - R relations that do not seem dependent on reinforcement in its usual sense. Evidently, the organism is "biased", through the phylogenesis of the species, towards developing these reactions.

Thus, only with biologically neutral S - R relations, is it possible to predict differential courses of habituation solely as a function of quantifiable aspects of the stimuli, reinforcers, and the particular modes by which they are administered. This is so because the organism is "un-prepared" (Seligman, 1970) for establishing such S - R relations and hence is susceptible to a wider range of artificial influences, particularly if these are introduced late in the ontogenesis. In these cases the concept of extinction would be applicable.

On the other hand, if species-specific responses of evident adaptive value are considered, the effects of ontogenetically early influences - preceding experimental manipulation - can not be disregarded when the same predictions are made. In these cases the organism is "prepared" and the effects of experimental manipulation can not be predicted without relating them to the natural early influences.For such S - R relations, habituation would be an appropriate term for response-waning.

As shown in this thesis, differential predictions can be made on the course of habituation of a species-specific response merely by interpreting the consequences of habituation in functional terms. However, if all major influences that govern its development and later plasticity are traced and described in quantifiable terms, the waning of this response would properly be labeled extinction.

It follows from these arguments that the more of the factors governing the plasticity of an S - R relation become identi-

fied and described in quantifiable terms, the waning of the response would simultaneously be less appropriately labeled habituation and more appropriately called extinction. The inconvenience of such a practice seems to justify an interchangeable use of these terms or to restrict the use of habituation to neuronal responses while extinction is referred to as a behavioral process (cf. Nyström, 1970).

Prospects

The suggestion that the early massive experience of the begging-call is a contributory determinant of the later observed withdrawal elicited by the 'seet'-call is based on inference rather than empirical data. Consequently, further experimentation should include broods that either are deprived of exposure to the begging-call and/or are subjected to the 'seet'-call to the same extent and preferably in the same context (associated with feeding). Such a study would provide an opportunity to evaluate the relative impacts of prenatal and early postnatal influences on later preferences for auditory stimuli.

The main response employed - cessation of begging - has been quantified only indirectly, using duration of begging in blind trials as a reference. A physiological correlate to the begging→neutral state→cease-begging dimension would provide a supplementary measure of the relative strength and progressive change of the motivation to approach (begging) or withdraw (cease-begging). A preliminary analysis of data on the heart-rate in GT nestlings during exposure to the 'seet'-call immediately after and between feedings, shows that the heart-rate increases markedly during begging and goes up further at cessation of begging when the 'seet'-call is replayed. This reaction is also shown when the same stimulus is administered between feedings. At the very least, this finding shows that the recorded abscence of begging can rightly be classified as a response when quantified in relation to the unmanipula-

ted duration of begging.

A differential responsiveness to auditory stimuli of varying significance, as measured by increases in heart rate, has been shown for other species (e.g. the Starling Sturnus vulgaris; Thomson et. al., 1968). Such studies provide an opportunity to relate stimulus significance, as derived from functional analyses, with measurable response-characteristics. Furthermore, by simultaneously recording behavioral habituation and a physiological correlate, changes in level of arousal can be related to behavioral changes. An application of this procedure would show, for instance, whether differences in excitatory level remain after behavioral habituation has taken place.

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